PATCH FORMATION AMONG ISRAELI CRUCIFERS: HOW DO THEY GET AWAY WITH IT?[1]

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Abstract

Many crucifers in the Mediterranean and desert floras of Israel frequently form large monospecific patches but do not suffer severe herbivore damage. This situation is unexpected from some recent theory of insect–plant interactions which predicts that such resource concentration should attract high herbivore loads, and that herbaceous plants should rely on unpredictability in time and space as a defense against herbivores. In Israel, Mediterranean crucifers flower earlier than members of other species-rich families with similar growth forms (Lamiaceae, Asteraceae, Liliaceae, Solanaceae, Poaceae, Papilionaceae, Apiaceae). This is not true for desert crucifers; their phenologies are unpredictable from year to year. We hypothesize that their displaced phenologies and possession of potent allelochemicals allow Mediterranean patch-forming species to produce monocultures while not sustaining high levels of herbivory. In contrast, desert patch-forming crucifers rely on unpredictable phenologies as well as allelochemicals as defenses against herbivores. Patch formation may be reinforced by plant–pollinator interactions. Among Mediterranean crucifers, patch formers are taller and have larger petals than do non-patch formers. In addition, patch formation is correlated with high levels of floral ultraviolet reflectance and patterning. These differences may result from reduced interspecific but enhanced intraspecific competition for pollinators among patch formers. These patterns are not found among desert species, although desert patch formers do initiate flowering before other crucifers.

The family Brassicaceae (Cruciferae) has figured prominently in the development of theory concerning insect–plant interactions. Responses of phytophagous insects to experimental manipulations of one or a few crucifer species (e.g., Tahvanainen & Root, 1972; Root, 1973; Slansky & Feeny, 1977), as well as considerations of family-wide attributes (Feeny, 1976, 1977), comprise much of the empirical and theoretical support for concepts such as "associational resistance" (Tahvanainen & Root, 1972) and "plant apparency" (Feeny, 1976). Feeny (1977) also cited family-wide attributes of crucifers to support his contention that escape in time and space and allelochemic diversity protect herbaceous plants from potential herbivores. Several characteristics of crucifers make them particularly amenable for studies of herbivore–plant interactions. They are well represented in floras of many regions of the world (Hedge, 1976), all species thus far examined contain glucosinolates (Kjaer, 1976), and many species are important cultivated crops.

The family contains approximately 400 genera and 3,000 species, most of which are annual herbs (Vaughan et al., 1976). The Irano-Turanian region is home to about 900 crucifer species and was probably the center of origin for at least the Old World taxa (Hedge, 1976). Brassicaceae is a dominant and conspicuous family in terms of species diversity and abundance in both the Mediterranean and desert regions of Israel, particularly in late winter and early spring (Shmida & Auerbach, 1983). Most of the 111 or more species native to Israel are Irano-Turanian or are descendants of Irano-Turanian stock (Zohary, 1973).

Crucifers frequently form enormous monospecific patches in Israel without sustaining extensive herbivore damage. This situation is unexpected from some current theory of insect–plant interactions which predicts that such resource concentration should attract high herbivore loads, and that herbaceous plants should rely on unpredictability in time and space as a defense against herbivores. Here, we examine the crucifer flora of Mediterranean and desert regions of Israel in terms of plant morphology, phenology, and propensity of some species to occur naturally in large monocultures. In partic-

ular, we address the question, "how do patch formers avoid colonization by a high density and/ or diversity of phytophages"?

ISRAELI CRUCIFERS

We obtained data on plant species from *Flora Palaestina* (Zohary & Feinbrun-Dothan, 1966), herbarium records of the Hebrew University Department of Botany, Hebrew University, field observations from January to June 1983, more than 10 years of vegetation samples taken by A.S., and phenological records from ECOPAS. The last is a computer data base compiled by members of the Department of Botany, Hebrew University, and the Society for the Protection of Nature in Israel. Each month phenological records are submitted by a network of observers, resulting in a comprehensive record of Israel's flora.

Tables 1 and 2 list species of native crucifers growing in the Mediterranean (76 species) and desert regions (37 species) of Israel (two species are listed in both regions). For each species we show growth form, floral characteristics, pubescence, abundance in Israel, and a subjective measure of size of monospecific patches. Within both assemblages we excluded extremely rare species that we never encountered in the field (approximately 20 species).

We must clarify one entry in Tables 1 and 2. Our index of patch formation ranges from "+ + +" (largest patches) to "−" (no patches). Although this categorization is subjective, we classified species as patch formers only if they formed large monospecific associations. A patch in our usage is not a clump of several individuals of one species; rather, it is an extensive single-species association. Patches range from approximately ten meters to several kilometers on a side. For instance, in spring 1983 (highest spring rainfall in 30 years), we measured patches of *Erucaria hispanica* L., near Arad, Israel, and *Sinapis arvensis* L., near Bet She'an, Israel, that extended several hundred meters from secondary roads and ran parallel to the roads for greater than three kilometers (further descriptions of locations can be found in Shmida & Auerbach, 1983). We combined all patch formers for statistical analyses.

Using these data, we compared phenological attributes of the Brassicaceae with those of seven other species-rich families with similar growth forms in Israel (Table 3). Phenological compar-

isons were based on peak flowering time (month in which most individuals of a species produce most of their flowers) and on range of flowering time (range of months in which flowers have been observed for each species). For each family we constructed cumulative frequency distributions of flowering range and peak and compared the resultant distributions using a nonparametric test of association (Kolmogorov-Smirnov 2 sample test, Conover, 1980). We also compared average month of peak flowering between the Brassicaceae and other families with a parametric test (Welch approximation of the *t*-test, Remington & Schork, 1970), since these data were approximately normally distributed. We limited these comparisons to Mediterranean species because desert species are constrained to flowering over a short, variable period when rains occur. Comparisons were done on all species and the subset of annual species for each family, except for Liliaceae which only has one annual species.

We then compared morphological and phenological attributes of patch- and non-patch-forming crucifers. These analyses were conducted separately for Mediterranean and desert species. We compared phenologies based on cumulative frequency distributions of flowering range and flowering peak and average month of peak flowering. In addition, we compared the average month of start of flowering using a parametric test (Welch approximation of *t*-test). Average plant height and petal size from ECOPAS were compared using *t*-tests, whereas analyses of associations of pubescence and ultraviolet patterns with patch formation were based on two-by-two contingency tables.

RESULTS

INTERFAMILY DIFFERENCES

Comparison of the phenology of Mediterranean crucifers with members of other families indicates that in general crucifers flower earlier in the year, both in terms of flowering range and flowering peak (Table 3). The single exception is no significant difference between the peak flowering time of the Brassicaceae and Liliaceae (Table 3). The average duration of flowering of all crucifers differs from that of all Lamiaceae, Asteraceae, Solanaceae, and Poaceae (Table 3). Among all families we examined, medians of flowering range and peak occur earlier for annual species than for perennials except for the Solanaceae, in which the situation is reversed. Peren-

TABLE 1. Morphological and ecological attributes of crucifer species in the Mediterranean flora of Israel. Growth form: A = annual; H = hemicryptophyte; CHN = between hemicryptophyte and chamaephyte; CH = chamaephyte. Flower phenology = months in which a species flowers (1 = Jan., 2 = Feb., etc.). Flower color: W = white; Y = yellow; CY = pale yellow; C = cream; F = flesh; P = purple; PP = pink; CP = pale pink. Relative abundance: O = 1–3 occurrences; RR = very rare; R = rare; C = common; LC = locally common; CC = very common.

Species	Growth Form	Mean Height (cm)	Pubescence	Flower Phenology	Flower Color	Petal Length (mm)	Relative Abundance	Patchiness
Aethionema carneum (Banks et Sol.) B. Fedtsch.	A	12	–	2–3	PP	2	RR	–
A. heterocarpum Gay	A	12	–	2–3	PP	2	C	–
Alyssum damascenum Boiss. et Gaill.	A	8	+	2–4	C	2	C	–
A. minus Rothm.	A	10	+	1–3	C	2	CC	–
Arabidopsis pumila (Stephan ex Willd.) Busch	A	13	–	2–3	C	2	O	–
A. thaliana Schur	A	15	–	2–3	W	2	RR	–
Arabis aucheri Boiss.	A	17	+	2–4	W	5	R	–
A. caucasica Schltr.	H	20	+	4–5	W	13	O	–
A. nova Villars	A	12	–	2–3	W	4	O	–
A. turrita L.	H	60	++	4–6	F	11	RR	–
A. verna (L.) R. Br.	A	15	+	3–4	W	7	C	–
Biscutella didyma L.	A	27	+	1–4	CY	3	CC	–
Brassica cretica Guss.	CHN	60	–	4–5	C	12	O	–
B. nigra (L.) Koch	A	120	–	4–6	Y	10	LC	+++
B. tournefortii Gouan	A	80	–	2–4	C	7	CC	+
Cakile maritima Scop.	A	30	–	3–11	P	9	CC	+
Calepina irregularis (Asso) Thell.	A	18	–	1–3	W	3	C	–
Capsella bursa-pastoris (L.) Medikus	A	18	–	12–4	W	2	CC	–
C. rubella Reuter	A	15	–	1–2	W	2	O	–
Cardamine hirsuta L.	A	20	–	2–4	W	2	RR	–
Cardaria draba (L.) Desv.	H	27	+	3–4	W	3	LC	+++
Carrichtera annua (L.) DC.	A	15	++	3–4	W	9	LC	–
Chorispora purpurascens (Banks et Sol.) Eig	A	25	+	3–4	P	18	RR	+
Clypeola aspera (Grauer) Turrill	A	10	+	1–3	C	2	R	–
C. jonthlaspi L.	A	8	++	1–3	C	2	CC	–
C. lappacea Boiss.	A	10	++	1–3	C	2	RR	–
Conringia orientalis (L.) Andrz.	A	50	–	3–4	Y	10	O	–
Coronopus squamatus (Forsskal) Asch.	A	10	–	2–4	W	2	LC	+
Crambe hispanica L.	A	65	+	3–4	W	3	C	+
Descurainia sophia (L.) Webb ex Prantl	A	25	+	2–4	C	3	O	–
Diplotaxis erucoides (L.) DC.	A	40	–	1–3	W	15	C	+++

Table 1.   Continued.

Species	Growth Form	Mean Height (cm)	Pubescence	Flower Phenology	Flower Color	Petal Length (mm)	Relative Abundance	Patchiness
D. viminea (L.) DC.	A	10	–	12–2	C	3	LC	–
Enarthrocarpus arcuatus Labill.	A	25	+	1–4	CP	13	LC	+
Erophila minima C. A. Meyer	A	6	–	1–3	W	2	CC	–
E. verna (L.) Besser	A	7	–	1–3	W	2	LC	–
Eruca sativa Miller	A	40	–	2–3	CP	17	LC	++
Erucaria hispanica (L.) Druce	A	50	–	2–4	P	12	LC	+++
Erysimum crassipes Fischer et C. Meyer	H	50	+	5–6	C	8	C	–
E. repandum L.	A	20	+	3–4	Y	7	R	–
Fibigia clypeata (L.) Medikus	CHN	35	++	2–4	Y	15	LC	++
Hesperis pendula DC.	H	55	++	4–6	F	17	R	–
Hirschfeldia incana (L.) Lagr.-Fossat	A	60	–	3–5	Y	10	CC	+++
Hymenolobus procumbens (L.) Nutt. ex Torrey et A. Gray	A	13	–	1–2	W	1	RR	–
Iberis acutiloba Bertol.	A	8	–	2–4	W	2	RR	–
Isatis lusitanica L.	A	50	–	2–4	Y	4	C	++
Lepidium latifolium L.	H	70	–	5–8	W	2	RR	–
L. ruderale L.	A	15	–	2–3	W	1	O	–
L. sativum L.	A	45	–	3–5	W	2	RR	+
L. spinescens DC.	A	40	–	3–5	P	2	LC	++
L. spinosum Ard.	A	25	–	3–5	W	2	R	–
Malcolmia chia (L.) DC.	A	15	+	2–4	P	10	C	–
M. crenulata (DC.) Boiss.	A	12	–	1–3	W	20	C	–
Maresia nana (DC.) Battand.	A	10	+	2–3	P	4	R	–
M. pulchella (DC.) O. Schulz	A	15	–	1–3	P	12	C	+++
Matthiola longipetala (Vent.) DC.	A	40	++	3–4	P	18	R	–
M. tricuspidata (L.) R. Br.	A	20	++	3–9	P	15	C	–
Myagrum perfoliatum L.	A	40	–	3–4	Y	4	O	–
Nasturtium officinale R. Br.	H	30	–	2–12	W	3	C	++
Neslia apiculata Fischer, C. Meyer et Avé-Lall.	A	40	+	2–3	Y	3	R	–
Ochthodium aegyptiacum (L.) DC.	A	70	–	2–4	Y	4	C	++
Peltaria angustifolia DC.	H	65	–	3–5	W	4	LC	++
Raphanus aucheri Boiss.	A	45	+	4–5	Y	11	C	–
R. raphanistrum L.	A	55	–	1–4	CP	18	C	++

TABLE 1. Continued.

Species	Growth Form	Mean Height (cm)	Pubescence	Flower Phenology	Flower Color	Petal Length (mm)	Relative Abundance	Patchiness
R. rostratus DC.	A	60	–	2–4	P	20	LC	++
Rapistrum rugosum (L.) All.	A	60	–	3–4	Y	8	C	++
Ricotia lunaria (L.) DC.	A	22	–	1–3	P	15	LC	++
Rorippa amphibia (L.) Besser	H	40	–	4–5	Y	5	O	–
Sinapis alba L.	A	100	+	3–4	Y	12	CC	++
S. arvensis L.	A	50	+	2–5	Y	9	C	+++
Sisymbrium damascenum Boiss. et Gaill.	A	45	–	2–4	Y	5	RR	+
S. irio L.	A	40	–	1–5	C	3	CC	+
S. officinale (L.) Scop.	A	40	+	3–4	Y	4	R	–
S. orientale L.	A	50	+	3–4	Y	9	R	–
Thlaspi arvense L.	A	30	–	3–3	W	4	RR	–
T. perfoliatum L.	A	8	–	1–3	W	3	CC	–
Turritis laxa (Sibth. et Smith) Hayek	H	60	–	4–6	W	5	RR	–

nials also have longer average durations of flowering than annuals, except in the Solanaceae.

INTRAFAMILY COMPARISONS

Tables 1 and 2 show that most crucifer species in Israel, as in other areas, are annuals. As mentioned above, the few perennial species in both the Mediterranean and desert floras generally flower later and longer than the annuals, although exceptions do exist (e.g., *Fibigia clypeata* L.). Additionally, a distinct guild can be recognized among both Mediterranean and desert species. This *Erophilla* or 'pygmy' guild is characterized by small plants (5–15 cm), with small, generally white or cream-colored flowers that appear early in the year (mid January through February). Within the two floral associations, we conducted all statistical analyses on crucifers four times: all species, annuals only, pygmy guild excluded, and perennials and pygmies excluded.

For the Mediterranean crucifers, patch-forming species are taller than non-patch-forming species (Table 4). In addition, height of patch formers generally paralleled our rank of patch formation ($+++ > ++ > + > -$, cases 3 and 4; $++ > +++ > + > -$, cases 1 and 2, Table 4). In three of four comparisons, patch formers also had significantly larger petals than did non-patch formers (Table 4), with patch rank generally paralleling petal size ($++ > +++ > + > -$, all cases). Few systematic differences exist among phenologies; patch formers generally do not flower earlier or longer than non-patch formers, although there are a few exceptions. There is no dominant flower color among Mediterranean patch-forming species; yellow, white, cream, and purple flowers are all common. Pubescence is significantly associated with non-patch-forming species in all analyses.

Unlike Mediterranean species, the desert patch-forming species are neither taller nor have larger petals than non-patch formers (Table 4). Although patch formers initiate flowering earlier than non-patch formers, the overall distributions of flowering peaks and ranges, and average durations of flowering generally do not differ between the groups.

Patch formers in the desert, with the exception of pygmy species, generally have purple flowers (8 of 12 species). Once again, pubescence is significantly associated with non-patch-forming species (Table 4).

Horovitz & Cohen (1972) analyzed ultraviolet

TABLE 2. Morphological and ecological attributes of crucifer species in the desert flora of Israel. See legend of Table 1 for abbreviations.

Species	Growth Form	Mean Height (cm)	Pubescence	Flower Phenology	Flower Color	Petal Length (mm)	Relative Abundance	Patchiness
Alyssum dasycarpum Stephan ex Willd.	A	10	+	2–4	C	3	RR	–
A. linifolium Stephan ex Willd.	A	10	–	1–3	W	2	R	–
A. marginatum Steudel ex Boiss.	A	10	+	2–4	C	2	R	–
A. minus (L.) Rothm.	A	10	+	2–3	C	2	C	–
Anastatica hierochuntica L.	A	5	+	2–4	W	3	R	++
Carrichtera annua (L.) DC.	A	15	++	3–4	C	9	LC	–
Cordylocarpus muricatus Desf.	A	37	+	3–4	C	8	O	–
Diplotaxis acris (Forsskal) Boiss.	A	35	–	1–4	P	10	C	++
D. harra (Forsskal) Boiss.	A	35	+	2–6	Y	9	CC	–
Enarthrocarpus strangulatus Boiss.	A	30	+	1–4	C	12	LC	+
Eremobium aegyptiacum (Sprengel) Asch. et Schweinf. ex Boiss.	P	15	+	2–6	PP	6	C	–
Erucaria boveana Coss.	A	35	–	2–4	P	10	CC	++
E. uncata (Boiss.) Asch. et Schweinf.	A	32	–	3–4	P	11	R	++
Farsetia aegyptiaca Turra	CH	35	+	1–11	F	12	CC	–
Isatis microcarpa Gay ex Boiss.	A	20	–	3–4	Y	3	RR	–
Leptaleum filifolium (Willd.) DC.	A	4	–	1–3	PP	7	C	++
Lobularia arabica (Boiss.) Muschler	A	12	–	1–4	W	4	LC	–
L. libyca (Viv.) Webb et Berth.	A	15	+	1–3	W	4	R	–
Malcolmia africana (L.) R. Br.	A	16	+	2–4	P	8	R	–
Maresia pygmaea (Del.) O. Schulz	A	7	–	3–4	P	9	R	–
Matthiola arabica Boiss.	H	40	++	3–5	F	12	RR	+++
M. aspera Boiss.	A	30	++	2–4	P	13	LC	+
M. livida (Del.) DC.	A	33	++	2–4	F	12	C	–
M. parviflora (Schousboe) R. Br.	A	17	+++	3–4	P	8	R	–
Morettia canescens Boiss.	CH	23	+++	2–10	W	8	LR	–
M. parviflora Boiss.	CH	20	+++	2–10	W	4	LR	–
Moricandia nitens (Viv.) E. A. Durrand et G. Barratte	CH	32	–	1–12	P	18	CC	+
M. sinaica (Boiss.) Boiss.	CH	60	–	3–4	P	12	RR	–
Nasturtiopsis arabica Boiss.	A	15	–	2–4	Y	3	CC	+++
Notoceras bicorne (Sol.) Caruel	A	5	+	1–3	C	2	CC	+
Pseuderucaria clavata (Boiss. et Reuter) O. Schulz	A	30	–	2–4	P	17	LR	+++

TABLE 2.   Continued.

Species	Growth Form	Mean Height (cm)	Pubescence	Flower Phenology	Flower Color	Petal Length (mm)	Relative Abundance	Patchiness
Reboudia pinnata (Viv.) O. Schulz	A	23	−	1–4	PP	9	CC	++
Savignya parviflora (Del.) Webb	A	20	−	2–4	P	5	LC	++
Schimpera arabica Hochst. et Steud. ex Boiss.	A	25	−	2–4	Y	3	LC	++
Sisymbrium erysimoides Desf.	A	30	−	1–5	Y	4	C	++
Torularia torulosa (Desf.) O. Schulz	A	15	+	2–4	W	3	LC	−
Zilla spinosa (L.) Prantl	P	35	−	2–9	P	13	CC	+++

characteristics of the flowers of 22 species of crucifers native to Israel (17 Mediterranean, 5 desert). Among these, high ultraviolet reflectance and/or patterning is positively associated with patch formation ($G_{adj.} = 12.3$, $P < 0.001$). The same is true for the subset of Mediterranean species ($G_{adj.} = 6.59$, $P < 0.025$), but not the desert ones ($G_{adj.} = 0.5$, $P > 0.05$).

DISCUSSION

WHY NOT FORM PATCHES?

Several lines of evidence suggest that patch formation should increase the susceptibility of a plant species to insect attack. Many herbivores, particularly those with narrow host ranges, are more likely to find, to remain on, and to reproduce on hosts that are concentrated in space (Root, 1973; Risch, 1981). This is one reason why monocultures of herbaceous plants frequently support greater densities of insect pests than do polycultures (Pimentel, 1961; Root, 1973; Feeny, 1976; Altieri et al., 1977; Risch, 1981). The diversity and abundance of phytophagous insects attacking a plant species in a given area are also influenced by the botanical diversity of the area (Strong et al., 1984). Members of a mixed-species plant assemblage often escape attack because increased species diversity reduces the susceptibility of each plant species to discovery. This phenomenon has been referred to as "associational resistance" (Tahvanainen & Root, 1972) or "plant defense guilds" (Atsatt & O'Dowd, 1976). Considerations of alternative resource availability for phytophagous insects as well as their frequent use of visual or chemosensory cues in host-plant location suggest that this form of escape should increase in effectiveness as phytophage dietary specialization increases (Root, 1973; Atsatt & O'Dowd, 1976).

Rhoades & Cates's (1976) and Feeny's (1976) general theories of plant defensive chemistry expand the concept of plant escape from enemies in ecological time into evolutionary arguments concerning selection for different classes of allelochemicals. Both postulate that as the occurrence of a plant species or tissue becomes more predictable (apparent) in space and time there should be greater selection for generalized, quantitative (dosage-dependent) defenses as opposed to specialized, qualitative defenses (toxins). Quantitative defenses are presumed to be more metabolically costly but harder for a herbivore to circumvent than qualitative ones. Thus, it is

TABLE 3. Comparison of phenologies of the Brassicaceae with other families in the Mediterranean flora of Israel. Months were converted to integers (Jan. = 1, Feb. = 2, etc.) for flowering range and peak analyses. Inequality signs indicate earlier (<) and later (>) in the growing season.

Family	Number of Species	Flowering Range (median month)	Flowering Peak (median month)	Flowering Duration (mean number months (s.d.))	Compared with Brassicaceae Flowering Range (distribution)	Compared with Brassicaceae Flowering Peak (distribution)
Brassicaceae	76	3.71	3.61	2.94 (1.47)		
Annual	64	3.46	3.52	2.88 (1.20)		
Perennial	12	5.50	4.75	—		
Lamiaceae	80	5.79	5.27	3.71 (1.49)*	> +	> +
Annual	17	4.86	4.42	3.35 (1.41)	> + +	> + +
Perennial	63	6.07	5.50	—	—	—
Asteraceae	169	5.74	4.88	3.43 (1.74)*	> +	> +
Annual	105	5.17	4.54	3.25 (1.69)	> + +	> + +
Perennial	64	6.63	5.83	—	—	—
Liliaceae	66	4.33	3.66	2.91 (1.34)	> +	=
Perennial	65	4.33	3.67	—	—	—
Solanaceae	15	6.96	6.50	5.13 (2.64)*	> +	> +
Annual	6	7.60	7.00	5.33 (0.82)**	> + +	> + +
Perennial	9	6.50	6.17	—	—	—
Poaceae	168	5.67	4.86	3.77 (1.95)*	> +	> +
Annual	111	5.18	4.59	3.40 (1.61)**	> + +	> + +
Perennial	57	6.65	5.68	—	—	—
Papilionaceae	206	4.52	4.19	3.13 (1.10)	> +	> +
Annual	173	4.33	4.08	2.92 (0.67)	> + +	> + +
Perennial	33	5.70	5.21	—	—	—
Apiaceae	87	5.35	4.83	3.03 (1.24)	> +	> +
Annual	48	4.93	4.55	2.77 (1.10)	> + +	> + +
Perennial	39	5.79	5.39	—	—	—

* = Significantly different from all, or annual (**) crucifer species (t-test, Welsh approximation, $P < 0.05$).
+ = Significantly different from all, or annual (+ +) crucifer species (Kolmogorov-Smirnov 2 sample test, $P < 0.05$).

argued that a plant that is apparent by virtue of its growth form, abundance, and longevity, such as a common tree species, must invest a considerable amount of energy into quantitative defenses, whereas an annual herbaceous plant can invest less energy in qualitative defenses, provided it also remains unapparent in time and/or space. By definition, unapparent plants should have small patch sizes and low population density (Fox, 1981).

Escape in time and space should be effective against specialized herbivores in ecological time and against nonspecialized herbivores over evolutionary time. Specialized herbivores that have evolved a means of circumventing an allelochemic defense frequently respond to the allelochemicals as chemosensory cues for host location and phagostimulation; such herbivores have, over evolutionary time, turned an unapparent re-

source into an apparent one (see Courtney, 1985, for various interpretations of apparency). Once this occurs the plant benefits from anything that reduces its apparency to adapted enemies, such as having an irregular phenology or growing in multispecies assemblages. Against nonspecialized herbivores, escape in space and/or time reduces the frequency of encounters between potential enemy and plant tissue, thereby decreasing the likelihood of an herbivore evolving a detoxification mechanism.

Since most crucifers are short-lived herbs and contain qualitative allelochemicals, one might expect them to rely quite heavily on escape in time and space from phytophagous insects. In fact, Feeny (1977) regarded crucifers as typical unapparent plants and much of his theory of plant apparency is based on crucifers (see references in Feeny, 1976). Most Israeli crucifers

do rely on escape on one time scale by nature of their annual growth form with concomitant short-term availability each year of leaves. However, the propensity of many species to form large monotypic patches confers a high degree of spatial predictability and resource concentration on these species. In addition, location of patches of Mediterranean patch-forming species frequently does not change from year to year. This situation would appear to be disadvantageous in light of the theory discussed above.

HOW DO THEY GET AWAY WITH IT?

Mediterranean patch-forming crucifers in Israel suffer little herbivore damage despite their short-term spatial predictability. During a season of sampling (1983), we never observed high densities or diversities of phytophages on patch-forming species. Neither high numbers of supported insect herbivores nor large amounts of leaf area removal were detected with spot censusing during ten years of vegetation sampling.

We suggest that Mediterranean patch-forming crucifers are able to grow and persist in dense monospecific associations owing to possession of glucosinolates (and other allelochemicals in some species), and because they flower earlier than other local species. Both displaced phenologies and glucosinolates prevent seasonal tracking and use of crucifers over evolutionary time by presently non-crucifer-adapted herbivores. By growing earlier than most other annual species, these crucifers have reduced the number of chance encounters with nonadapted phytophages; such occasional encounters deter or kill the insect. Therefore, we see a displaced phenology reinforcing defensive chemistry and thereby reducing the probability of evolved phenological and dietary shifts in phytophages. If patch formation occurred later in the growing season, more encounters between pest and potential host would ensue, and over evolutionary time one would expect an increase in diversity of insect species adapting to patch-forming crucifer species.

Many crucifers germinate, grow, and flower before the annual peak of insect biomass. Indeed, many of the patch-forming species flower before the annual appearance of crucifer-adapted herbivores, such as *Pieris brassicae, P. rapae,* and alticine flea beetles (Furth, 1979; Auerbach & Shmida, unpubl. data). Occasionally, these adapted herbivores do appear on patch formers during the late stages of flowering or seed set,

TABLE 4. Comparisons of morphological and phenological attributes of patch-forming (P) and non-patch-forming (NP) crucifer species in the (A) Mediterranean and (B) desert floras of Israel. In reference to phenological traits, the inequality signs indicate earlier (<) and later (>) in the growing season. Groups are defined as: (1) = all species; (2) = annuals; (3) = pygmy guild excluded; (4) perennials and pygmies excluded.

Group	Plant Height	Petal Size	Mean Flowering Duration	Flowering Peak (distribution)	Flowering Peak (mean)	Flowering Range (distribution)	Start of Flowering	Pubescence
(A) MEDITERRANEAN								
1	P > NP***	P > NP**	P > NP*	P = NP	P = NP	P = NP	P = NP	NP > P*
2	P > NP***	P > NP***	P = NP	P = NP	P > NP*	P = NP	P = NP	NP > P*
3	P > NP*	P = NP	P = NP	P = NP	P = NP	P = NP	P < NP*	NP > P*
4	P > NP***	P > NP*	P = NP	P = NP	P = NP	P = NP	P = NP	NP > P*
(B) DESERT								
1	P = NP	P = NP	P = NP	P = NP	P = NP	P = NP	P < NP*	NP > P**
2	P = NP	P = NP	P = NP	P = NP	P = NP	P = NP	P < NP**	NP > P*
3	P = NP	P = NP	P = NP	P = NP	P = NP	P = NP	P < NP*	NP > P**
4	P = NP	P = NP	P = NP	P = NP	P = NP	P = NP	P < NP**	NP > P*

* = Significant difference, $P < 0.05$; ** = $P < 0.01$; *** = $P < 0.001$.

when herbivory has a minimal effect on the fitness of annuals.

Germination timing in the desert is far less predictable than in Mediterranean regions because of variable late-winter and early-spring rains (Shmida et al., 1985). Thus, desert crucifers are far more unpredictable in time than their Mediterranean counterparts. Year-to-year variation in composition, location, and size of patches is often tremendous. Despite these differences, flowering is still well under way by the time most herbivores, even crucifer specialists, arrive. Interestingly, pubescence, a characteristic frequently interpreted as a possible herbivore defense (Coley, 1983) as well as an adaptation that reduces rates of evapotranspiration (Lieberman & Lieberman, 1984), is more common among non-patch- than patch-forming species in both floristic regions.

We can only speculate why crucifer-adapted herbivores have not undergone phenological displacement to exploit early-season crucifers. Selection for synchrony may be countered by physiological constraints associated with early-season cold temperatures. The extremely variable phenologies of desert crucifers also may preclude herbivore synchrony. As Feeny (1977) noted, "Short growth season, shifting pattern of geographic distribution, and association with harsh and somewhat unpredictable climatic conditions are all characteristics which are likely to favor escape by plants from their adapted enemies"; this has been echoed elsewhere (Janzen, 1970; Rhoades & Cates, 1976; Feeny, 1976). In addition, selective pressure for phenological changes among Mediterranean crucifer-feeding insects may not be very great, since cruciferous hosts are available later in the season. There also may be phytochemical barriers that function with phenology in much the same manner as we envisage for nonadapted herbivores. Many crucifers contain diverse glucosinolates as well as other allelochemicals, and the performance of crucifer feeders frequently varies greatly among host plants (Root & Olson, 1969; Feeny, 1976; Rodman & Chew, 1980).

HOW ARE PATCHES FORMED?

The ability to form patches clearly involves more than early phenologies, since we found few significant phenological differences between Mediterranean patch- and non-patch-forming crucifers (Table 4). In Mediterranean and desert regions of Israel, late-winter rains initiate germination of seeds of crucifers and other annuals. By early spring, patches of various crucifers dominate the landscape of much of Israel (Shmida & Auerbach, 1983). Bell & Muller (1973) described similar patch formation by an introduced crucifer, *Brassica nigra*, in some annual California grasslands. There, *B. nigra* produces monospecific patches throughout the grasslands despite synchronous germination of all annual species following late-autumn rains. Bell & Muller (1973) found that patch formation by *B. nigra* involves production of potent allelopathic chemicals. We do not know if allelopathy is important in patch formation by Israeli crucifers. Growth rate appears to have a role in patch formation. Many crucifers in Israel and elsewhere (Feeny, 1977) mature and set seed extremely rapidly, a trait associated with their occurrence in environmentally harsh or disturbed sites. In addition, patch formation may involve differential responses to microsite variability in edaphic parameters and grazing pressure.

WHY FORM PATCHES?

Patch formation may be reinforced by competition for pollinators and increased pollination efficiency. Most crucifers, including Israeli species, are either facultative or obligate outcrossers (Fryxell, 1957; Crisp, 1976; D. Zohary, pers. comm.). Seasonally advanced flowering among Mediterranean crucifers may reduce interspecific competition for pollinators, provided flowering does not occur before pollinators are available. Patch formation among these species may also increase pollination success over that of solitary individuals if pollinators are limited. Thus, patch formation could be reinforced by pollination success.

While patch formation may concentrate resources and produce attractive displays for pollinators (Handel, 1983; Rathcke, 1983), intraspecific competition for pollinators among members of a patch may increase if patch size becomes sufficiently large. For example, Rathcke's (1983) density-visitation model envisages a facilitation in pollination as patch size increases up to the point where pollinators are saturated, and thereafter an increase in competition with expanding patch size. Intraspecific competition for pollinators may also increase if advanced phenologies result in flowering before the annual peak in pollinator availability

(Schemske et al., 1978). As intraspecific competition intensifies, selection for enhanced attractiveness may result in differences between patch- and non-patch-forming species in pollination-associated traits.

In our analyses, two morphological attributes frequently associated with pollination, plant height and petal size (Faegri & van der Pijl, 1979; Waddington, 1979; Waser, 1983a), did vary between non-patch- and patch-forming species. Among Mediterranean species, patch formers are taller and they generally have larger petals than do non-patch-forming species. Although we do not know the intensity of intraspecific competition for pollinators in patches, increases in height and petal size were also positively associated with our measure of patch size. In addition, plant height, petal size, and indices of patch size were positively correlated with propensity for outcrossing as measured by pollen/ovule ratios (Kunin, unpubl. ms.). Thus, taller patch formers appear to have a greater tendency towards outcrossing than do smaller patch formers, and species that do not form patches have the lowest tendency to outcross. That high levels of ultraviolet reflectance and patterning is positively correlated with patch formation found among Mediterranean species also suggests that patch formation may result in increased intraspecific competition for pollinators.

Differences in height and petal size do not occur among desert species; however, desert patch-forming species do begin flowering before non-patch formers, a difference observed among Mediterranean species only when the early-flowering pygmy guild is excluded from analyses. Advanced flowering among the desert patch formers may reduce interspecific competition for pollinators (Waser, 1983b) and possibly permit pollinator specialization. Some pollinators in other deserts are capable of synchronizing with the ephemeral phenologies of their hosts (Baker & Hurd, 1968; Crawford, 1981). With the exception of the pygmy guild, a high proportion of desert patch formers have purple flowers (67% patch vs. 27% nonpatch), which suggests possible pollinator specialization or segregation between patch- and non-patch-forming species.

In summary, we suggest that growing in patches aids in pollinator attraction, especially in conjunction with atypical phenologies. Displaced phenologies also may function to segregate pollinator and herbivore guilds temporally. If pollinator efficiency is high and seed dispersal low, patch formation may be self-perpetuating, because of concentration of seeds into localized seed banks.

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